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Root Growth of Two Perennial Grass Types and Musk Thistle (*Carduus nutans*) in Temperate Grasslands of North America

Chengchou Han and Stephen L. Young*

Root architecture of prairie grasslands, which depends on plant phenology and edaphic conditions, strongly influences susceptibility to invasion by nonindigenous plant species. Field studies were conducted to compare in situ root growth patterns of warm-season (WS) and cool-season (CS) perennial grasses and musk thistle during a 2-yr period that included a drought in the second year. In 2 yr, CS grasses had the highest amount of roots (1,296 m roots m^{-2} [395 ft roots ft^{-2}]) across shallow (0 to 28 cm [0 to 11 in.]), medium (28 to 56 cm), and deep (56 to 98 cm) depths with 65% occurring in the shallow depths. However, roots of WS grasses were always greater at deeper depths compared to roots of CS grasses. The amount of new roots in CS grasses was statistically different in 2011 ($F_{2,43} = 33.3$, $P < 0.0001$) at all depths for vegetative (April to May), inflorescence (June), and dormant (July to November) stages. In 2012, the amount of new roots in CS and WS grasses was statistically different ($F_{2,60} = 81.7$, $P < 0.0001$ and $F_{2,37} = 8.0$, $P = 0.0013$), respectively, for vegetative (April to May), inflorescence (May to June), and dormant (June to November) stages. For both years, the amount of new roots in the CS grasses showed an interaction between the three growth stages and three soil depths ($F_{2,62} = 33.3$, $P < 0.0001$ [2011]; $F_{4,60} = 18.6$, $P < 0.0001$ [2012]). From germination to senescence, the total amount of musk thistle roots was 298 m roots m^{-2} , which was less than the CS (1,296 m roots m^{-2}) and WS (655 m roots m^{-2}) grasses. The largest proportion of new musk thistle roots (61%) ($F_{2,42} = 40.4$, $P < 0.0001$) occurred during the bolting stage (April to June) of the second year. These results show the difference in root distribution of two grass types and the niches that are created underground by extraneous conditions (e.g., drought) in WS grass stands that may contribute to the establishment of musk thistle, an invasive plant species in many North American regions.

Nomenclature: Musk thistle, *Carduus nutans* L. CRUNU.

Key words: Cool-season perennial grass, distribution, disturbance, drought, invasion, minirhizotron, warm-season perennial grass.

Invasive plants are commonly found in temperate grasslands of the central prairies of North America (Eddy and Moore 1998; Mico and Shay 2002; Smith and Knapp 2001). In these regions, native perennial grass resistance to nonindigenous plant species invasion depends on resource acquisition timing aboveground (e.g., light, moisture) and belowground (e.g., soil moisture, nutrient, biological soil space) (Blank and Morgan 2012; Daehler 2003; DiTomaso et al. 2003; Young et al. 2011). Root distribution patterns

of native perennial grasses and invasive plants are often influenced by the dominant habitat type and variations in carbon and nutrient cycles (Aerts et al. 1989; Jackson 1997). However, few studies have focused on root growth and development for a season or for the life cycle of an individual plant species in relation to the effects of management or naturally occurring conditions (see Fernandez and Caldwell 1975; Larreguy et al. 2012; Young et al. 2010). If a more thorough understanding of plant community resistance to invasion is expected, belowground activities and processes will need to be elucidated.

Restoring native perennial grass communities in temperate grasslands is desirable for maintaining functional diversity and ecosystem health. Several factors contribute to resistance to plant invasion. Root production and longevity of native plants are contributing factors (Berlinger and Knapp 1991; Bottoms and Whitson 1998; Laufenberg

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Management Implications

In established or newly restored grasslands, niches can occur that allow for the invasion of exotic plant species. This study examined root distribution patterns of cool-season and warm-season perennial grass species and musk thistle. Grown individually, cool-season perennial grasses had a greater number of active roots in the upper soil profile (0 to 28 cm), whereas warm-season perennial grasses had more roots that were active deeper (56 to 98 cm) in the soil. Musk thistle roots were found to dominate the upper soil profile (0 to 28 cm). Even though the two grasses and musk thistle were grown separately, predictions can be made relating to the potential for which grass type will be more susceptible to the invader. The lack of uniform root distribution in the upper soil profile by warm-season perennial grasses could contribute to the establishment of musk thistle. Further, under alternating years of normal and below-normal annual precipitation, musk thistle seedlings could germinate and grow as small rosettes in poorly managed grasslands during the first year (wet) and then continue rosette development, bolting, and flowering in the second year (drought) as roots are extended more fully throughout the soil profile. Therefore, land managers that have problems with musk thistle or an invasive plant species with similar life history (e.g., Scotch thistle, bull thistle) should consider (1) using a mix of perennial grass types and (2) not stressing grassland plants by overgrazing, especially during extreme drought conditions.

2003). Moreover, a plant community composed of a mixture of rooting architectures, to fully occupy soil space, also contributes to resistance. Perennial grass types in the central prairies, which are a large component of North American temperate grasslands, include both warm-season (WS; C4) and cool-season (CS; C3) species. Roots of many WS perennial grasses extend over 3 m (9.8 ft) into the soil profile, but many CS grasses have more fine roots that are concentrated in the 0- to 50-cm soil depth increment (Fransen et al 2006; Gist and Smith 1948; Weaver 1954).

Invasion theory postulates that resistance by native plant communities to invaders is due to an overlap in resource use patterns (Young et al. 2010, 2011). The overlap in resource acquisition occurs when the native and invasive plants compete for the same spatially or temporally available resources at specific phenological growth stages (Suding et al. 2003; Zavaleta and Hulvey 2007). An established, healthy, and diverse native perennial grass stand has an extensive root system that allows for the efficient uptake of resources with few open niches (Blank and Morgan 2012).

The growth and development of plant roots is affected by interspecific competition (Harris 1977) and abiotic factors such as available soil moisture (Canham et al. 2012), soil nutrients (Drew and Saker 1975), and adequate soil temperature (Steinaker et al. 2010; Teskey and Hinckley 1981; Tierney et al. 2003). DiTomaso et al. (2003) reported that a decrease in the availability of light aboveground corresponds to a reduction in root productivity for yellow starthistle (*Centaurea solstitialis* L.), an

invasive plant species in California. Blank and Morgan (2012) indicated that early season root growth of CS grasses reduced biological soil space for competitors and increased resistance to invasion by *Bromus tectorum* L.

For many temperate grasslands, disturbances such as overgrazing by livestock or extreme climate events (e.g., drought) may change the distribution and growth of plant roots. Repeated grazing at excessive stocking rates creates openings or niches in the aboveground canopy that allows for the establishment of invasive plant species (Feldman et al. 1968). Similarly, extreme drought events reduce soil moisture levels and cause alterations in plant growth that make native plant communities (e.g., grasslands) less competitive with invasive plant species (Meisner et al. 2013). Musk thistle (*Carduus nutans* L.), an herbaceous monocarpic species that was introduced to the United States from Eurasia, is able to take advantage of niches in grasslands that fail to recover from periods of excessive disturbance (Beck 1999; Hulbert 1986; Leininger 1988). As a biennial herb, musk thistle rosettes extend fine roots in shallow soil layers during the first year and develop large taproots deeper into the soil beginning in the second year (Rees et al. 1996). The pattern of musk thistle root growth and production may be an important factor that contributes to successful establishment in temperate grasslands.

In this study, we measured root lengths of musk thistle and WS and CS perennial grasses to determine root distribution patterns and suggest a potential niche for the establishment of the invader. Based on our previous studies (Young et al. 2010), we hypothesized that grass roots would be uniformly distributed throughout the soil profile more so than those of musk thistle. Further, we hypothesized that grasses would better endure drought, due to a root system more extensive than that of musk thistle.

Materials and Methods

Site Description. The study was conducted at the University of Nebraska–Lincoln West Central Research and Extension Center (WCREC) in North Platte, NE (41.090°N, 100.768°W), where average annual precipitation is 508 mm (20 in.) of which 80% occurs from late April to mid-October (USDA 1978). The total seasonal precipitation was 513 mm in 2011 and 113 mm in 2012, which was 3% higher and 77% lower, respectively, than the historical average (Figure 1).

Monthly precipitation and daily soil temperature were obtained from a weather station located at the WCREC and operated by University of Nebraska–Lincoln. The dominant soil type was a Cozad silt loam (fine-silty, mixed, mesic Fluventic haplustoll) (Payero et al. 2008). CS and WS perennial grass communities were established separately in 2007. In the WS perennial grass community, *Panicum virgatum* (switchgrass) was the dominant species

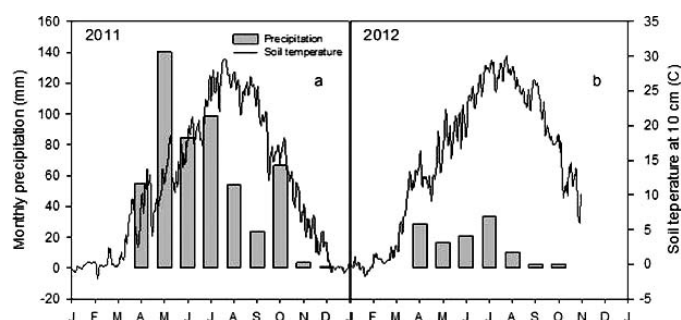


Figure 1. Monthly precipitation and soil temperature (10 cm) in 2011 and 2012 at the West Central Research and Extension Center in North Platte, NE.

at the beginning of the study with few individuals of *Andropogon gerardii* Vitman (big bluestem), *Schizachyrium scoparium* (Michx.) Nash (little bluestem), *Andropogon hallii* Hack (sand bluestem), *Sorghastrum nutans* (L.) Nash (Indiangrass), *Bouteloua curtipendula* (Michx.) Torr. (side-oats grama), *Desmanthus illinoensis* (Michx.) MacMill. ex B.L. Rob. & Fernald (Illinois bundleflower), *Dalea purpurea* Vent. (purple prairie clover), and *Lupinus perennis* L. (sundial lupine). In the CS perennial grass community, *Dactylis glomerata* L. (orchardgrass), *Bromus inermis* Leyss (smooth brome), and *Bromus riparius* Rehmann (meadow brome) were the dominant species in 2011 with only a few individual *Alopecurus arundinaceus* Poir (creeping meadow foxtail) plants. All grasses were seeded at rates according to recommended guidelines (Anderson 2007). Following planting, grass communities established to full canopy cover each year.

Musk thistle seeds were collected in 2010 near the WCREC. A preliminary germination test indicated seed viability was near 30% for the collection (data not shown). Seeds of musk thistle were sown in bare-ground plots and WS and CS grass plots. Three musk thistle seeds were hand-planted at points equidistant from neighboring points in each plot. Each plot was planted with 140 musk thistle seeds on April 28, 2011. Musk thistle seedlings emerged approximately 1 mo after planting and were allowed to grow naturally without disturbance.

Experimental Design. The CS and WS plantings were in separate but nearby locations that covered approximately 300 m² (3229 ft²) each and the WS planting area included a section of bare ground for establishing musk thistle monocultures (Figure 2). The grasses had been established within a limited area and, thus experimental units were selected randomly in each grass (WS and CS) and bare-ground area. Plot size was 5 by 2 m. Grass and musk thistle phenology was recorded throughout the main growing season (April through November) for the 2 yr by marking several representative plants and taking measurements biweekly (Table 1). Plant growth was averaged for each month.

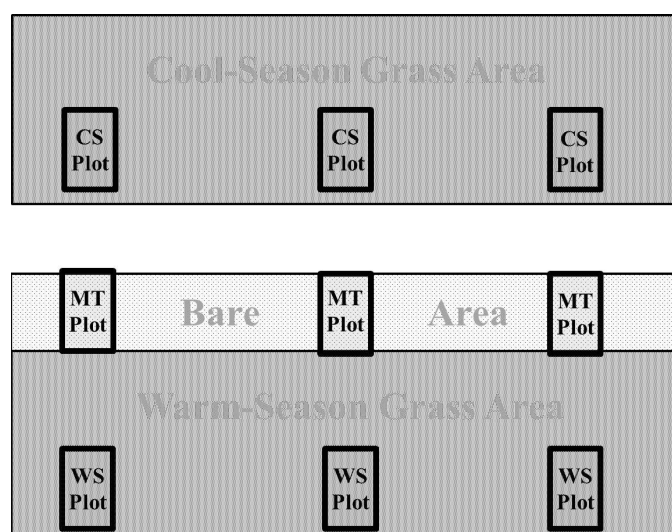


Figure 2. Field layout and approximate location of plots in cool-season (CS) and warm-season (WS) perennial grass, and bare ground areas. Musk thistle (MT) planted into the bare areas.

Late in 2010, three transparent butyrate minirhizotron tubes (180 cm [5.9 ft] in length and 6.4 cm in inner diam) were installed into WS, CS, and musk thistle plots (nine tubes total) to measure root growth each year. All tubes (with capped bottoms) were inserted into the soil to just above the surface using a power auger. The auger and tubes had the same outside diameter, thereby providing a tight fit for the tube with the surrounding soil. The tubes were inserted at a 45° angle from vertical. The top end of the tubes was sealed with a cap to prevent entry of rainwater and debris.

Root length measurements for fine roots (diam < 2 mm) were recorded using an electronic scanner (CI-600® In Situ Root Imager, CID Bio-Science, 4901 NW Camas Meadows Drive, Camas, WA 98607) attached to a laptop computer. The scanned areas of the soil, which included roots, were seven evenly spaced vertical depths (0 to 14, 14 to 28, 28 to 42, 42 to 56, 56 to 70, 70 to 84, and 84 to 98 cm) starting at the soil surface. We calculated actual root depths by using method similar to that of Torrión et al. (2012). The scanned images encompassed a 360° image around the tube at each depth. Each scanned image was transferred electronically to the computer for later analysis and conversion to root length per square meter. Roots were identified as old root (not white) and new root (white) in an image. Total root length was old and new roots. Root length from captured images in all seven depths was combined into categories referred to as shallow (0 to 28 cm), medium (28 to 56 cm), and deep (56 to 98 cm), which allowed for easier analysis of root growth patterns.

Images were collected similar to Johnson et al. (2001) and roots were quantified similar to Aerts et al. (1989) by outlining all visible roots on a computer touch screen display of the digitized images using specialized root

Table 1. Growth stages for cool-season and warm-season perennial grasses and musk thistle recorded throughout the main growing season (April through November) for 2 yr taking measurements biweekly and averaging stages for each month.

	April	May	June	July	August	September	October	November
2011								
Cool-season	Vegetative	Vegetative	Inflorescence	Dormant	Dormant	Dormant	Dormant	Dormant
Warm-season	Dormant	Vegetative	Vegetative	Vegetative	Inflorescence	Inflorescence	Dormant	Dormant
Musk thistle	Planted	Seedling	Rosette	Rosette	Rosette	Rosette	Dormant	Dormant
2012								
Cool-season	Vegetative	Inflorescence	Dormant	Dormant	Dormant	Dormant	Dormant	Dormant
Warm-season	Vegetative	Vegetative	Inflorescence	Dormant	Dormant	Dormant	Dormant	Dormant
Musk thistle	Bolting	Flowering	Flowering	Flowering	Senescence	Senescence	Senescence	Senescence

analysis software (CI-690 Rootsnap[®], CID Bio-Science). Root images were taken monthly starting in May 2011 and ending in September 2012, which coincided with senescence of musk thistle. No measurements were taken during winter when plants were dormant. Any plants other than the target species were hand removed biweekly from plots to prevent extraneous roots from appearing in images.

Statistical Analysis. Total root length or new root length was compared at shallow (0 to 28 cm), medium (28 to 56 cm), and deep (56 to 98 cm) depths using a mixed model in a repeated measure analysis. Due to variation in growing conditions and plant growth characteristics, data were analyzed separately for each year. All statistical analyses were conducted with the GLIMMIX procedure of SAS (SAS v. 9.1, SAS Institute, Cary, NC 27513).

Results and Discussion

In theory, root distribution patterns of plant species can be related to the phenology of plants distributed within a specified community (Steinaker et al. 2010). However, many abiotic factors can influence root growth and development in addition to physical obstructions, nutrient availability, and allelopathic interactions. Here, we focus on the abiotic factors, specifically precipitation and soil temperature, affecting perennial grass and musk thistle roots over a 16-mo period, which covered growth of the invader from germination to senescence.

During the 2 yr of this study, precipitation was highly variable, with normal conditions and extreme drought. For an entire year, monthly precipitation amounts for 2012 were dramatically lower than 2011 (Figure 1). In 2011, 30% of the yearly total precipitation amount occurred in May (140 mm) and almost 15% occurred in October (66 mm). The decline in annual precipitation that began at the end of 2011 and continued into much of 2012 created extensive water deficits, as most (89% or 100 mm) of the total precipitation for that year occurred in a very narrow 4-mo period of late spring and early summer.

Aboveground phenology and belowground root growth for all three plant types was strongly influenced by the two different precipitation patterns. Life cycles of WS and CS perennial grasses and even musk thistle were shortened in 2012 due to severe drought and a lack of soil moisture. Musk thistle completed most vegetative growth during the year of normal precipitation. In the drought year, the perennial grasses either accessed soil moisture sooner in the season or deeper in the soil profile. Had the drought occurred in the first year, a different response from all plant types would have been expected. Nevertheless, precipitation patterns constantly vary and measuring plant response during any two or more consecutive years when conditions change or remain the same can be helpful for identifying mechanisms that facilitate survival by one plant type compared to another.

The amount of total roots for CS grasses was different ($P < 0.0001$) for the three soil depths (0 to 28, 28 to 56, and 56 to 98 cm) in both 2011 and 2012 (Figure 3; Table 2). This was also true for the total amount of WS grass roots (Figure 3; Table 2). For the 2 yr, the amount of new roots only for the CS grasses was significantly different for growth stage ($P < 0.0001$) and soil depth ($P < 0.0001$) (Figure 4; Table 3). The amount of new musk thistle roots was significantly different, but this was due to depth in 2011 (year 1) and growth stage in 2012 (year 2) (Figure 5; Table 3). Except for CS roots at deep depths, the amount of new roots for all plant types declined beginning in May or later of the second year (Figures 3–5).

In both years, WS grasses had a greater amount of roots in the medium and deep depths compared to the shallow depth. WS grasses had the greatest amount of roots (total and new) at the medium depth during the vegetative stage (May–July) in 2011 and at the deep depth during the inflorescence stage (June) in 2012 (Figure 4). In 2012, the amount of new roots declined at all three depths as drought conditions intensified in June during the inflorescence stage.

The amount of CS grass roots differed substantially among the three different soil depths (0 to 28, 28 to 56,

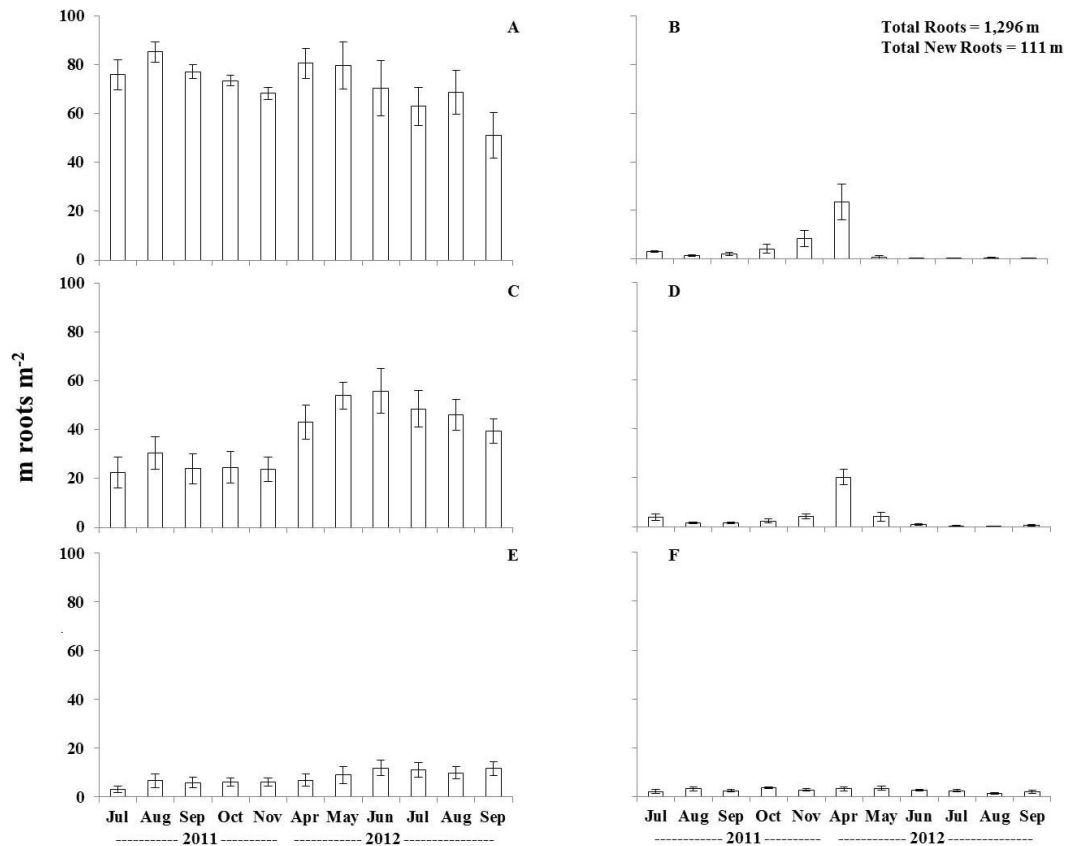


Figure 3. Roots for cool-season perennial grasses at (A, B) shallow (0 to 28 cm), (C, D) medium (28 to 56 cm), and (E, F) deep (56 to 98 cm) depths. Both total (A, C, E) and new (B, D, F) roots are shown for the 2-yr period. Bars represent ± 1 SE.

Table 2. Test of fixed effects on total root length in 2011 and 2012. Growth stages for cool- and warm-season perennial grass included vegetative, inflorescence, and dormancy, whereas musk thistle stages included seedling, rosette, dormancy, bolt, flower, and senescence. Depths measured were shallow (0 to 28 cm), medium (28 to 56 cm), and deep (56 to 98 cm). F values are significantly different at $P < 0.05$ and $P < 0.001$.

Treatment	Factor ^a											
	Growth stage				Depth				Stage by depth			
	Num	Den	F	Pr > F	Num	Den	F	Pr > F	Num	Den	F	Pr > F
	DF	DF			DF	DF			DF	DF		
2011												
Cool-season	1	63	1.21	0.2761	2	63	380.1	< 0.0001**	2	63	3.7	0.0302*
Warm-season	2	41	1.11	0.3403	2	41	27.01	< 0.0001**	4	41	1.71	0.1674
Musk thistle	1	37	0.08	0.7723	2	37	0.36	0.6977	2	37	0.48	0.6228
2012												
Cool-season	2	60	2.29	0.1096	2	60	166.4	< 0.0001**	4	60	3.2	0.0189*
Warm-season	2	43	4.65	0.0148*	2	43	32.31	< 0.0001**	4	43	0.2	0.9352
Musk thistle	2	37	2.84	0.0712	2	37	3.24	0.0504*	4	37	0.98	0.432

^aAbbreviations: Num Df, numerator degrees of freedom; den DF, denominator degrees of freedom; Pr, probability.

* $P < 0.05$; ** $P < 0.001$.

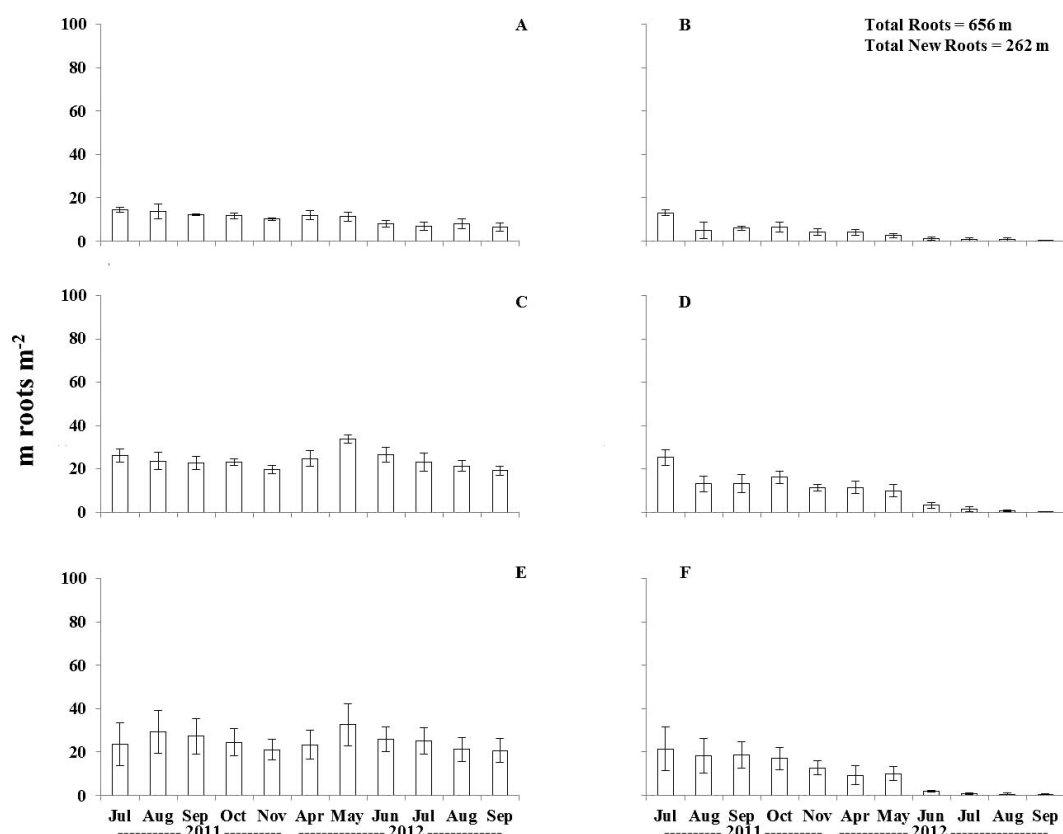


Figure 4. Roots for warm-season perennial grasses at (A, B) shallow (0 to 28 cm), (C, D) medium (28 to 56 cm), and (E, F) deep (56 to 98 cm) depths . Both total (A, C, E) and new (B, D, F) roots are shown for the 2-yr period. Bars represent ± 1 SE.

Table 3. Test of fixed effects on new root length in 2011 and 2012. Growth stages for cool- and warm-season perennial grass included vegetative, inflorescence, and dormancy, whereas musk thistle stages included seedling, rosette, dormancy, bolt, flower, and senescence. Depths measured were shallow (0 to 28 cm), medium (28 to 56 cm), and deep (56 to 98 cm). F values are significantly different at $P < 0.01$, and $P < 0.001$.

Treatment	Factor ^a											
	Growth stage				Depth				Stage by depth			
	Num DF	Den DF	F	Pr > F	Num DF	Den DF	F	Pr > F	Num DF	Den DF	F	Pr > F
2011												
Cool-season	1	62	74.22	< 0.0001**	2	62	40.38	< 0.0001**	2	62	33.28	< 0.0001**
Warm-season	1	37	0.32	0.577	2	37	0.46	0.6334	2	37	0.3	0.7411
Musk thistle	2	41	9.02	0.0006**	2	41	25.24	< 0.0001**	4	41	2.09	0.1002
2012												
Cool-season	2	60	81.72	< 0.0001**	2	60	11.68	< 0.0001**	4	60	18.63	< 0.0001**
Warm-season	2	37	8.01	0.0013*	2	37	0.71	0.4994	4	37	0.1	0.9801
Musk thistle	2	42	40.4	< 0.0001**	2	42	6.24	0.0042*	4	42	4.08	0.0069*

^a Abbreviations: Num Df, numerator degrees of freedom; den DF, denominator degrees of freedom; Pr, probability.

* $P < 0.01$; ** $P < 0.001$.

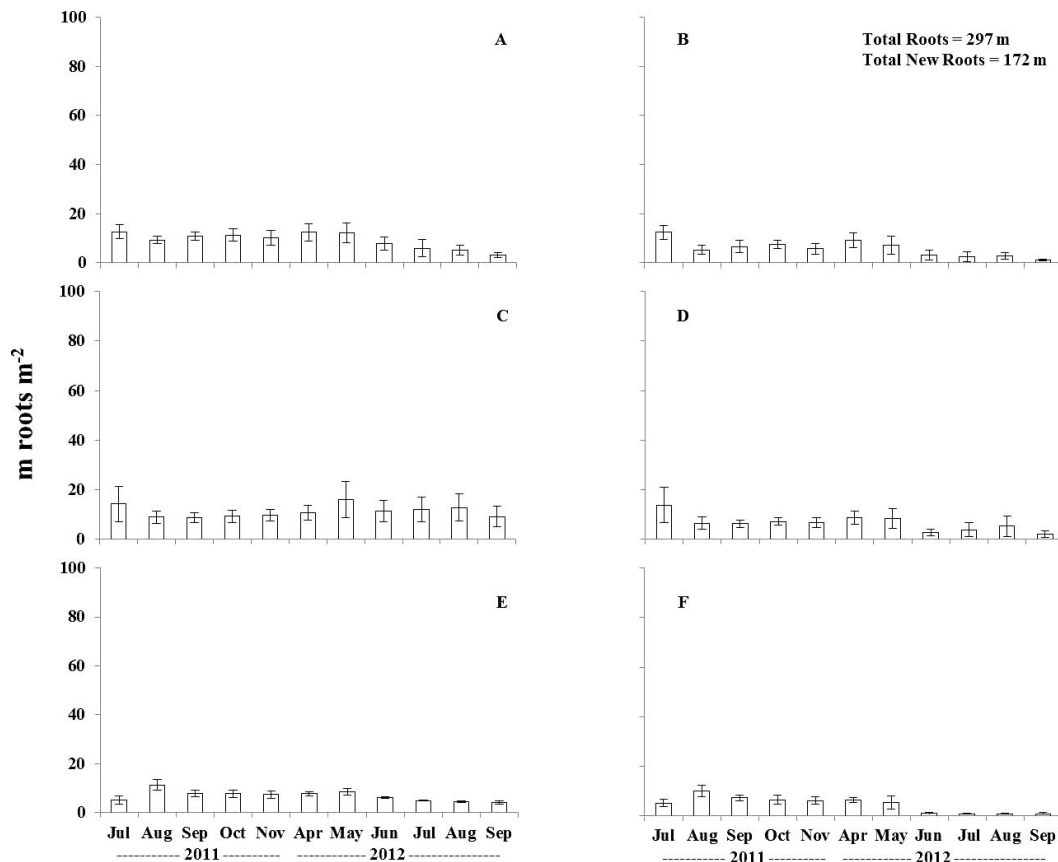


Figure 5. Roots for musk thistle at (A, B) shallow (0 to 28 cm), (C, D) medium (28 to 56 cm), and (E, F) deep (56-98 cm) depths. Both total (A, C, E) and new (B, D, F) roots are shown for the 2-yr period. Bars represent ± 1 SE.

and 56 to 98 cm) with the highest in the shallow depth (0 to 28 cm) (Figure 3). With increasing soil depth, the amount of roots declined. The amount of total roots in the shallow and medium (28 to 56 cm) depths decreased after the inflorescence stage (May) in 2012 when drought conditions intensified. The amount of new CS grass roots remained fairly constant at deep depths (56 to 98 cm), even during drought conditions. The amount of CS grasses roots (old and new) was at least four times higher than WS grasses and musk thistle at the shallow depth (0 to 28 cm) in 2011 and 2012.

The total amount of WS grass roots was greater than that of CS grasses at soil depths deeper than 28 cm. The highest proportion (70 to 80%) of roots for most WS perennial grass species has been found to be in the upper 30 cm of soil (Kitchen et al. 2009; Kucera and Dahlman 1968; Weaver and Darland 1949). However, the remaining roots that are distributed deeper in the soil may have a greater physiological importance than shallow roots for accessing available moisture, especially during drought. Tufekcioglu (1999) reported that roots of switchgrass were widely distributed in deep soil layers. The switchgrass ecotype 'Trailblazer', which is an upland type that was used in our

study, has a bunching growth habit and few spreading rhizomes. The amount of roots of WS grasses was associated with sufficient soil moisture levels in the first year (Figure 4). In the second year, the amount of total roots of WS grasses began higher or at a similar amount as the previous year, but decreased as the drought conditions intensified starting in midseason (May) and continuing through the end of the season. The amount of new roots of WS grasses declined similar to amounts of CS grass and musk thistle roots in the second year due a lack of soil moisture. Some grasses are especially sensitive to soil moisture variation and tend not to produce new roots when soil moisture fluctuates or remains low (Hild et al. 2001).

The CS grasses had the highest amount of roots at shallow depths (0 to 28 cm), which is typical of sod-forming grasses, such as *B. inermis*. The amount of new roots in the shallow depths for the CS grasses was greatest earlier in the season before June of the first year and May of the second year (vegetative stage, prior to inflorescence) when soil temperatures were cooler, which may indicate that higher temperatures later in the season may have affected the amount of CS grass roots. Liu and Huang (2005) found that high soil temperatures hinder the

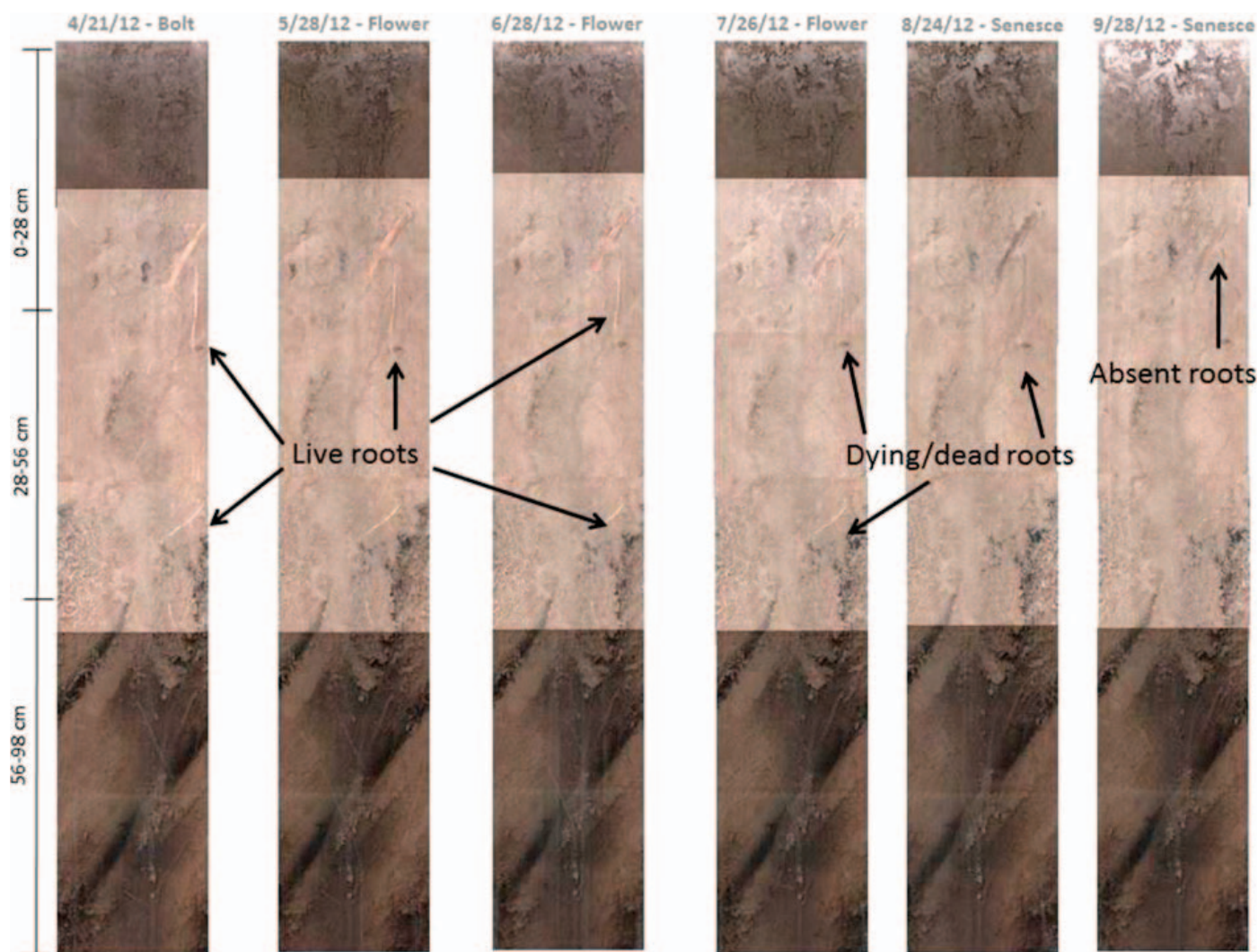


Figure 6. Images in situ of musk thistle roots using a minirhizotron camera during the second year of growth.

development of CS grass roots and Xu and Huang (2000) reported 49 d of high air/soil temperature (20/35 °C) reduced the number of creeping bentgrass (*Agrostis palustris* Huds. 'Penncross') roots from 12 to 2 cm⁻² at shallow (5 to 7 cm) soil depths.

In May 2011, musk thistle germinated from seed that had been planted in April. Most of the plants developed into rosettes and from June to September remained vegetative before becoming dormant in late fall. Of the 84 musk thistle plants that established in all of the plots, a very small number (3.5%) flowered and set seed in the first year. In 2012, musk thistle that had established in the previous year completed a biennial life cycle, which is typical for the plant species (Roeth et al. 2003). During the second year, musk thistle rosettes emerged from dormancy and began to bolt at the end of April. Mature plants reached a maximum height of 180 cm in July, as flowering spanned the months of June through August.

The amount of roots of musk thistle were lower compared to the grasses (Figure 5), except at deep depths for CS and shallow depths for WS grasses. Although there was no difference in the amount of total roots across soil depths (0 to 28, 28 to 56, and 56 to 98 cm) or growth stages for musk thistle in 2011 or 2012 (Table 2), the amount of new roots was significantly different in both years (Table 3). The amount of new roots declined noticeably in June 2012 after the flowering stage, even though some roots, albeit dead, still remained (Figure 6).

Musk thistle produced the least amount of roots compared to the two perennial grasses. This could have been due to the short longevity of musk thistle roots (e.g., biennial) and the production of a main tap root that may not be easily captured in images taken in a stationary tube belowground. We addressed these two issues by installing tubes well in advance of seeding musk thistle into plots and placing the tubes at a 45° angle positioned directly

underneath the location of the sown seed. Musk thistle was established and reached more than 90% cover in September in 2011 and most of the plants kept developing in 2012. Interestingly, the amount of new roots for musk thistle was greater than that of the CS grasses at the medium and deep depths and the WS grasses at the shallow depths. These results indicate that a greater proportion of the total amount of musk thistle roots (old and new) was alive and active for the 2-yr period. In addition, Rees et al. (1996) reported musk thistle can extend tap roots quickly into soil following emergence from dormancy in the spring of the second year, which was similar to our results (bolting stage; Figure 6). As a short-lived herb, the shallow roots of musk thistle may facilitate its invasion into WS grasses, which have fewer roots distributed in the upper soil profile. Also, rapid root expansion may facilitate musk thistle invasion into bare ground or overgrazed sites that have little competing vegetation.

In 2011, grasses in the WS communities emerged from dormancy in June and by August, plants had reached full inflorescence. By the end of the season, the grasses in the WS treatments reached a maximum height of 150 cm. In 2012, maximum WS perennial grass height was 50 cm by mid-June, which remained unchanged for the remainder of the season. Average maximum CS grass height was 35 cm in both years. The CS grasses displayed dormant-like appearance or less overall growth in 2012, due to the extreme drought conditions.

Some perennial grass species are able to avoid drought by maturing more rapidly (Weaver and Clements 1938). However, we found no evidence that would suggest rapid aboveground phenological development related to a proliferation or dramatic reduction in belowground activity, only that the amount of roots appeared to decline because of a lack of soil moisture. Had there been two consecutive years of normal precipitation, we would have been able to test this in a long-term study by comparing root lengths from years with normal precipitation to those from years when drought occurred. Nevertheless, during the two study years, a lack of soil moisture recharge at the end of 2011 and into 2012 negatively affected root length in the WS and CS grasses and musk thistle. The new grass roots present early in the second season (April and May), rapidly turned brown after June with increasing temperatures and continued lack of soil moisture.

After disturbance, there is an increase in the potential for musk thistle to invade WS and CS grasses assuming the amount of roots decreases and aboveground biomass is reduced. For disturbances related to drought (Qian et al. 1997; Reeder and Schuman 2002), we found a different response in the amounts WS and CS grass roots. During drought conditions, the amount of new grass roots decreased to near zero later in the season, except deep in the soil where WS grasses may extend roots down to 3 m. The amount of total grass roots decreased gradually between the year of

normal precipitation and drought. Regardless of whether drought conditions subside or persist in the years following, a niche has been opened in the upper soil profiles of WS and CS grasses that could potentially allow for musk thistle invasion and establishment.

The use of perennial grasses by land managers for grassland restoration should include a consideration for the belowground occupancy that may help in the prevention of encroaching invasive plant species. Abiotic factors such as drought and temperature that affect grassland health could result in less resistance to musk thistle invasion. Switchgrass and other WS grasses tend to have bunch-forming growth, shorter rhizomes, and fewer shallow roots that may allow musk thistle seedlings to establish in openings or niches exposed by disturbance that would otherwise be closed (Han and Young 2014). In contrast, the sod-forming roots of the CS grasses provide dense roots and rhizomes in the shallow and middle soil depths that may be able to restrict shallow root development by newly germinating musk thistle plants.

Our study sheds light on how musk thistle invasion into two different perennial grass types could be dependent on root distribution patterns of the invader and the grass and the importance of disturbance type (e.g., drought), which may lead to successful or failed establishment. Other than soil moisture, the variability in available resources, physical obstructions, and beneficial microorganisms are all associated with root distribution patterns and may further impact the successful establishment of an invasive plant species such as musk thistle. Young et al. (2011) reported that native perennial grass water use patterns were plastic (e.g., variable) when annual precipitation amounts changed between years. Alternatively, Eggemeyer et al. (2008) reported that a woody plant species, eastern redcedar (*Juniperus virginiana*), and WS perennial grasses competed for water in the upper soil profile, but cedar showed plasticity in water uptake deep in the soil as seasons changed from early spring to midsummer. In this case, the grasses were not able to compensate and compete with the cedar. Considering that research on root growth and development of perennial grasslands and invasive plant species is fairly limited (Jackson et al. 2001), our study is important in elucidating the impacts of disturbances to prevent a reduction in long-term function and health of these systems by the establishment of invasive plant species.

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